

## AN ANALYSIS OF POPULATION STRUCTURE IN PACIFIC MOLE CRABS (*HIPPA PACIFICA* DANA)

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*Hippa pacifica* Dana, a hippid mole crab, inhabits the intertidal zone of tropical and subtropical Pacific island beaches. At Oahu, Hawaii, it primarily scavenges *Physalia*, the Portuguese man-of-war which washes onto beaches from the open ocean (Matthews, 1955; Wenner, 1977). At Enewetak Atoll, Marshall Islands, although it sometimes receives an abundance of *Physalia* (S. Smith, personal communication), the mole crab apparently depends more upon lagoon-produced mysids and other zooplankton which wash ashore at night (Wenner, 1977).

A comparison of population samples in this species, both in Hawaii and at Enewetak, provided some unexpected observations. In Hawaii, samples of *Hippa pacifica* suggested a remarkably consistent population structure. During a 5-month period, samples were essentially identical to one another, whether obtained from different beaches or from different parts of the same beach on Oahu. However, the consistent results obtained in Hawaii did not hold for extensive sampling at Enewetak Atoll. Samples from populations on different beaches at that atoll showed wide differences when sex ratio was analyzed as a function of crab size.

Wenner (1972) earlier had examined the question of sex ratio and size for many marine crustaceans. At that time he conjectured that the several distinct patterns found might be species-specific, on the basis of data available. However, this hypothesis failed with the initial comparison of data from Hawaiian and Enewetak mole crab samples. Hawaiian population samples fell into what had been termed an "intermediate" pattern, whereas the first year's samples at Enewetak formed the "reversal" pattern found in protandrous species such as the pandalid shrimps studied by Butler (see Wenner, 1972; Fig. 8).

The second year of sampling at Enewetak yielded conflicting data among various islets and led to a reconsideration of the premise that the sampling method provided representative data, even though this discrepancy among samples was not initially obviously related to sampling method (the same procedure had been used in all cases). To test the efficacy of sampling technique, a beach of limited extent was sampled at Enewetak in the usual manner, except that animals were not returned as had been done earlier. Instead, crabs were removed during a 3-week period until few or no crabs came to the individual bait stakes (sampling with removal). Initial samples, which represented the normal sampling procedure, could then be compared with the larger segment of population removed from the beach. The question became: In what ways did the initial samples represent the larger beach population?

### MATERIALS AND METHODS

The study site at Enewetak Islet was a 250-m long beach which terminated on its eastern end at a solid-walled cargo pier and tapered in the other direction to

a narrow strip of sand among concrete blocks and limestone rubble. Much of the western half of the beach fronted a limestone reef flat. At low tides the sand on that portion of the beach bordered on exposed coral reef.

During a 3-week period in 18 separate sessions (1–2 hr each), a total of 4011 animals was removed from the beach with the use of a baiting procedure described fully by Wenner (1977). Stakes baited with shark meat and placed approximately 10 m apart along the entire stretch of beach during each sampling session attracted the crabs. Thirty to forty stakes were kept in the sand for approximately 20 min and were reset two or three times more during each session.

Mole crabs, apparently reacting to chemical stimuli (Matthews, 1955), scurried toward the bait as it was repeatedly covered by wave action. Successive sets of bait during each sampling session usually yielded progressively fewer animals per bait stake. By the end of each session, even fresh bait placed between the sampling stakes did not generate an increase in catch rate.

Animals were usually collected during the mid-point of an outgoing tide, because that appeared to be the optimal time (on the basis of earlier experience). They were occasionally collected during other parts of the tidal cycle in order to sample sand patches covered by water only at such times. Such attempts, however, never yielded as many animals per unit effort as did those run during outgoing tides. Accordingly, in some comparisons samples were grouped by twos in order to offset those small numbers and to better reveal trends.

After animals were sieved from the sand, they were measured with the aid of an automatic sizing device (Wenner, Fusaro, and Oaten, 1974). Tallies included size, sex, and percentage of females carrying eggs within each size class. Females were returned alive to beaches at the opposite end of the islet. Males were kept in a sea water table and eventually returned alive to the original beach as part of another experiment.

## RESULTS

### *Changes in catch during removal*

Animals, when considered by sex and size, did not come uniformly to the bait during the 3-week period. The overall catch of males fluctuated until mid-way through the program and then began tapering off (Fig. 1A). By contrast, female catch was greatest at first, with a rather consistent decline thereafter (Fig. 1B). Small females (those equivalent in size to the male size range—solid bars in Fig. 1B) showed much the same catch pattern as males, however, indicating that size rather than sex was the factor responsible for the differences in catch pattern between males and females.

One prominent feature of the change which occurred during the removal program was the selective catch of large females during the early part of that period (Figs. 1B, C). More than 80% of the 378 females caught in the first two samples were greater than 12.4-mm carapace length (the mean minimum size of egg-carrying females). In the last six samples, however, fewer than 18% of the females caught were at least that large (N = 319).

The percentage of those females larger than 12.4-mm carapace length which carried eggs also varied at the removal beach during the 3-week period (Fig. 1D).

In the first two samples combined, 64.2% of the 307 larger females carried eggs, whereas 85.0% of the remaining number of larger females had eggs ( $N = 860$ ). A 9 by 2  $\chi^2$  test for homogeneity failed ( $\chi^2 = 77.00$ ,  $P < 0.001$ ), indicating that the percentage of egg-carrying females changed significantly during the 3-week period. Since egg development time is approximately 20 days (unpublished results), such a change with time would not be unexpected.

Results from the other two islets which had been repeatedly sampled yielded somewhat more consistent data. At Jedrol (David) Islet, where the removal program was started later and run only 10 days, the percentages of large females in berry for the five samples were 87.2, 85.7, 86.0, and 83.6%, respectively, with data for the last two samples combined to eliminate small sample error ( $N = 376, 434, 150$ , and 116, respectively). Those percentages did not show a significant change with time ( $\chi^2 = 1.05$ ,  $P < 0.05$ ). At Boken Islet, two samples taken 6 days apart had 89.3 and 84.2% of the larger females in berry ( $N = 337$  and 505, respectively), a marginal significant difference ( $\chi^2 = 4.53$ ,  $P < 0.05$ ).

Sex ratio fluctuated more markedly than any other variable measured during the removal program. The first three of the 18 samples yielded a total of 923 animals, with each of those three having a low percentage of males (27.7, 28.2, and 30.1%, respectively). In later samples the percentage of males varied widely, from a low of 40.6% males (fifth sample) to a high of 78.8% males (last sample). However, a persistent upward trend in that percentage became evident when the percentage of males was considered as a function of cumulative number of animals caught (Fig. 1E). Beginning with the fourth sample, the overall percentage of males increased uniformly. After 4011 animals had been collected, 48.4% of them were males. When those data were grouped into four blocks of 923, 1127, 896, and 1065 animals, a 4 by 2  $\chi^2$  test yielded a value of 234.36 ( $P < 0.001$ ). When the same test was run with the first group omitted, the data remained heterogeneous ( $\chi^2 = 113.00$ ,  $P < 0.001$ ). This level of significance, coupled with the close fit of the line to the points, indicates that males were under-represented in the first group of three samples and over-abundant in the last group of 1065 animals (last seven samples combined).

It was after the trend shown in Figure 1E began to emerge that a total of 1679 animals was removed from the beach on Jedrol (Rex) Islet, where a parallel set of results emerged (Fig. 1F). Unfortunately, time did not permit additional sampling at that islet.

Two samples from Boken (Irwin) Islet were also obtained. The male percentage there rose from 1.7 to 6.4% during removal of a total of 346 and 456 animals, respectively. Boken Islet differs from the other two in being downwind from the lagoon waters during trade wind conditions and is, presumably, in a more food-rich location (Fusaro, 1978b; Wenner, 1977).

#### *Estimates of population size*

Since catch per unit effort generally declined during removal trapping, and since rate of decline is directly related to size of total population and to number removed, the total population size can be estimated by various methods (Southwood, 1966, pp. 181-186). However, not all of the four conditions as listed by

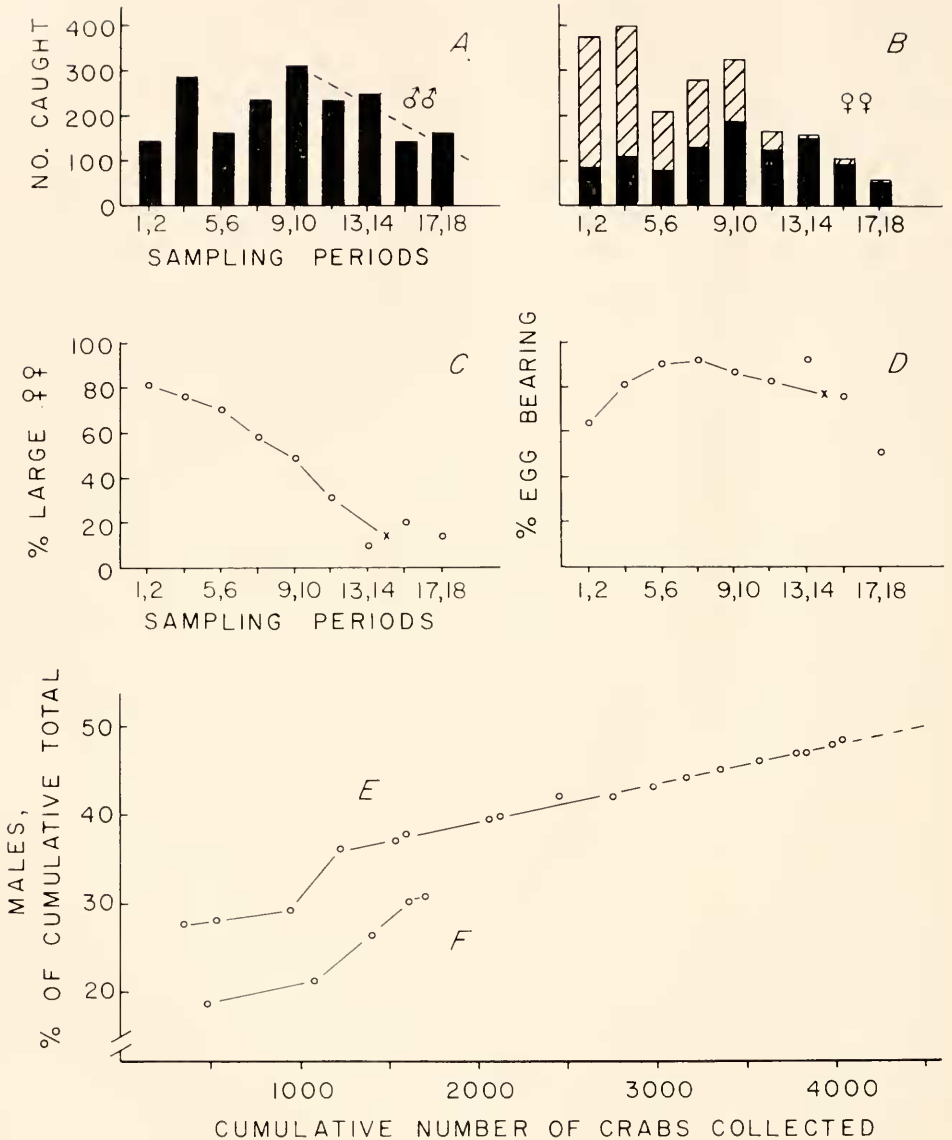


FIGURE 1. Changes in population samples during the three-week removal program. The bars depict sequential male (A) and female (B) catches, with the 18 samples grouped in pairs. Hours spent collecting each pair of samples were: 2, 2, 2, 2.25, 4, 2.5, 2.5, 3 and 3, respectively. The dashed line in Figure 1A indicates a consistent decline in catch per unit effort starting midway through the removal program; the solid portion of each bar in Figure 1B represents small females (females  $\leq 12.5$ -mm carapace length, the mean maximum size of males). The line in Figure 1C shows the decline in percentage of females which were large (females  $\geq 12.4$ -mm carapace length, the mean minimum size at onset of egg-bearing), while Figure 1D illustrates the differences obtained in egg-bearing percentages for those larger females during

TABLE I

*Various estimates of the number of animals inhabiting the study beach on Enewetak Islet, determined by different methods based upon changes in catch pattern during removal sampling.*

Method	Estimates of total population size			
	males	Total females	Small females	Total animals
Max. likelihood ( $\pm$ s.e.)	9575 ( $\pm$ 2996)	2374 ( $\pm$ 35)	6091 ( $\pm$ 6182)	6279 ( $\pm$ 208)
Regression "Corrected Regression"	8661	2532	4859	6539
Time-Unit 1:1 Sex ratio	2661	2389	1271	4658
	2967	2223	1518	4752
	2250	2250		4500
Total caught	1940	2071	1008	4011

Southwood (1966) were met in this present study. One condition in particular, "The chance of being caught must be equal for all animals" was clearly violated; males and small females were not caught as readily in the first eight sessions as were large females (first four bars in Figs. 1A, B). Nevertheless, a use of the various methods did provide a set of estimates (Table I), from which inferences can be drawn. In each case, estimates were made independently from the data for males, females, small females, and total number of animals, on the basis that the catch patterns differed markedly from one another in those different categories.

The method based on maximum likelihood, which Southwood (1966) called "the most accurate method", yielded the least consistent set of results. The male estimate ( $9575 \pm 2995$ ) exceeded the estimate for total number of animals ( $6279 \pm 208$ ). Likewise, the calculated number for small females exceeded the number estimated for all females.

Use of the regression method initially provided the same lack of consistency as that yielded by the maximum likelihood method; estimates for the number of males and small females were far too high to correspond with the estimates for total numbers of all animals or of all females. By inspection of Figures 1A and 1B, on the other hand, such a result would be expected, since males and small females clearly began a consistent decline in numbers only after the first eight samples (first four bars in those figures) had been removed from the beach.

Alternatively, one can adapt the regression method by applying it to the data

sequential removal. In both Figures 1C and 1D a weighted mean ( $\bar{x}$ ) for the last three paired points compensates for small sample variation. The line in Figure 1E represents the percentage of males as a function of cumulative number of animals caught in the 18 samples at the main removal beach, while the line in Figure 1F shows the same relationship for animals taken from Jedrol Islet.



for the last 10 samples (last five bars). The estimates derived in each case can be added to the numbers caught in the first eight samples. Serious inconsistencies then disappear ("corrected regression" in Table I).

The "time-unit" method for estimating population size (Kono, in Southwood, 1966) relies heavily on data obtained at only three times (as well as on the cumulative catch at those times): the first sample, the mid-point sample, and the last sample. An application of that method to the data yielded estimates relatively close to those produced by the "corrected regression" method, with males and small females again being somewhat over-estimated because of their under-representation in the first sample.

Finally, if one assumes a 1:1 sex ratio for the population (the megalopa stage of *Emerita analoga* arrives on the beach in a 1:1 sex ratio, Wenner, 1972), an extrapolation of the line in Figure 1E to the 50% mark would yield an estimate of about 4500 animals. The 2250 females so estimated (assuming a 1:1 sex ratio) closely matches each of the other estimates for the total number of females.

The various estimates shown in Table I, qualified by the nature of the violation of conditions outlined by Southwood (1966), would indicate that most of the animals were removed from the study beach (between 87% and 93%, particularly if one relies on the quite consistent set of results for the total number of females).

The foregoing analysis now permits an assessment of how well the initial samples represented the larger beach population.

#### *Modal size classes*

The data for all samples combined fell into discrete modal size classes (Fig. 2), when separated by the method outlined by Cassie (1954). Data for males separated cleanly into only three modes, with the third mode having a slight inflection above the 95% level. The steep slope of Mode 3 suggests a maximum size for that sex. Female data actually fell into five modes. However, since the third and fourth modes did not differ appreciably, those data were combined and were thereafter treated as Mode 3 (Figs. 2, 3). The data thus reveal that the beach likely experienced four or five periods of recruitment during the year or two prior to sampling. (It should be noted, however, that the mode of largest females is based upon only seven animals caught during the first three sampling periods.)

To illustrate some of the differences in modal size class structure which arose during the removal process, data from the first three samples ( $N = 923$ ) are herein compared to data obtained from the last six samples ( $N = 876$ ). In all cases, modes were again separated by the same method.

Females in the first three samples ( $N = 657$ ) fell primarily into the four or five modes mentioned earlier (Fig. 3A), but females in the last three samples ( $N = 319$ ) provided data for only three distinct modes (Fig. 3B). The large displacement in the two sets of lines in Figure 3 does not represent an appreciable change in the size of animals within each mode. Rather, the displacement reflects a change in relative *percentage* of females which fell into each of the three modal size classes when one compares the beginning and end of the 3-week sampling period. For example, as can be seen in Figure 3, most females in the first three samples were in the third mode (79% of 657 females), whereas the second mode contained

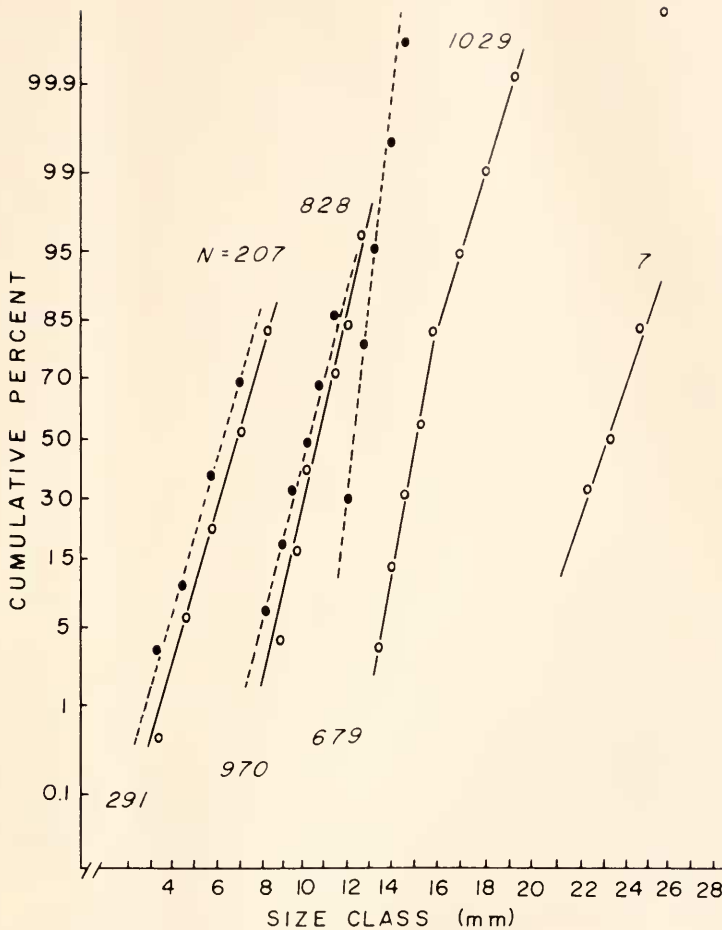


FIGURE 2. Male and female modal size classes for all data ( $N = 4011$ ). Males (broken lines) fell into three distinct size classes when modes were separated by the method of Cassie (1954). Females (solid lines) continued growth beyond the maximum male size. Approximate numbers within each mode are indicated below each line representing male modes and above each line representing female modes.

most of the females in the last six samples (72% of 319 females). Thus, two facets of modal size class structure should be distinguished: first, the estimated mean size of animals within each mode and second, the relative percentage of animals within each mode.

The data derived from the captured males (Fig. 4) differed from that for females in some important respects. Only two male modes occurred in the first three samples combined (Fig. 4A), while four or five female modes were evident in those combined samples (Fig. 3A). The smallest and largest females had no counterpart among the males in the first three samples. However, the last six

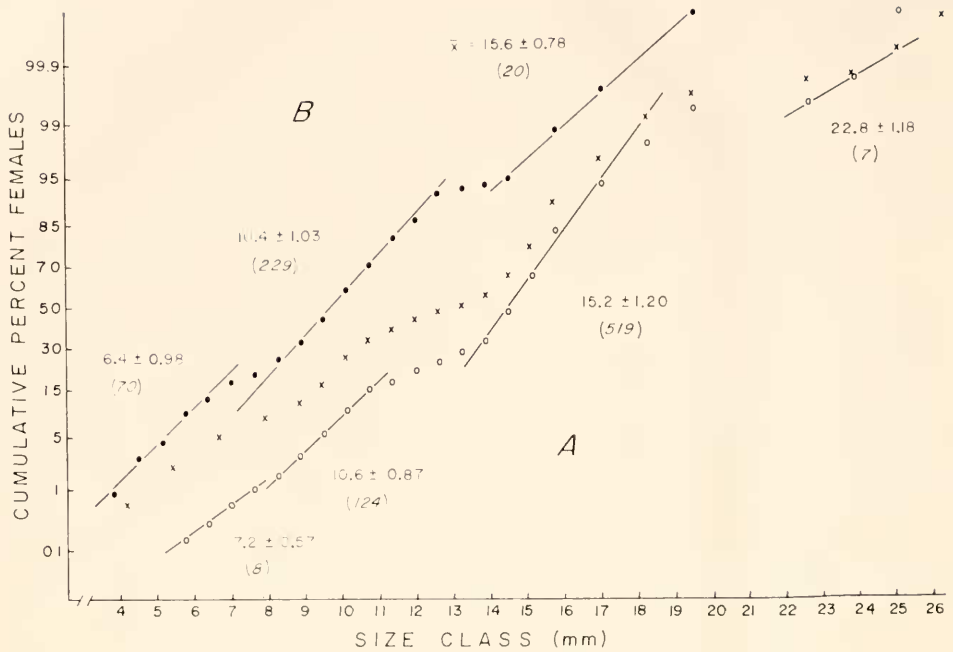


FIGURE 3. Changes in cumulative percentage of females as a function of size during removal. Data for the first three samples combined (open circles) fell into at least four modes (A). Data from the last six samples (closed circles) formed only three discrete modes, displaced upward on the graph due to a later catch of a higher percentage of smaller females (B). The  $x$  symbols indicate the relationship for all female size data ( $N = 2071$ ). The sets of numbers below the lines indicate means, standard deviations, and approximate number (in parentheses) of animals within each mode in Figure 3A, and the numbers above the lines represent the same characteristics for Figure 3B. (See Fig. 2 for separation of modes for the total female data.)

samples yielded three modes for the males (Fig. 4B), modes which could be matched quite readily with the three modes representing smaller females in Figures 2 and 3B.

On the other hand, data for males obtained in the first three and in the last six samples (Fig. 4) did not show that same parallel relationship found in the female data (Fig. 3). The lines representing the upper mode for males in first and last samples converged. S. R. Haley (personal communication) and M. Page (personal communication) have concluded from laboratory results that males reach a maximum size and cease growth, though they continue molting. Females in the laboratory, according to Haley and Page, showed no such cessation of growth under similar circumstances.

The relative percentage of males which fell into each mode also differed markedly in the first and last samples (Fig. 4). The upper (third) mode in the first three samples contained approximately 75% of the 266 males, while 61% of the 557 males caught in the last six samples were in the second mode.



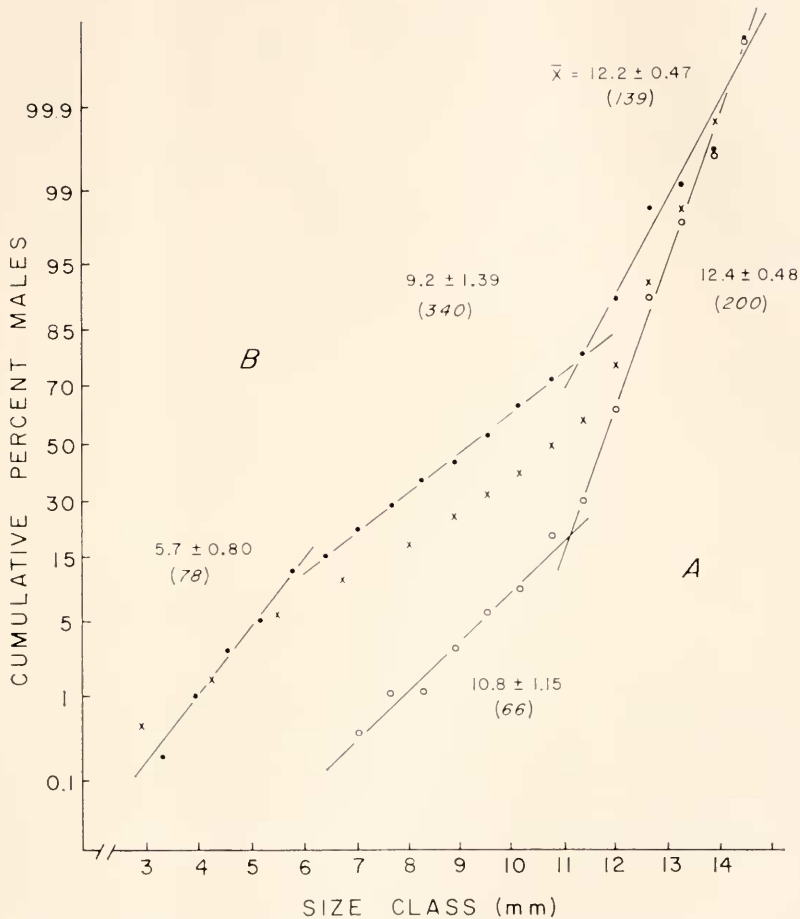


FIGURE 4. Changes which occurred in cumulative percentages of males, as in Figure 3 for females. Initial samples (A) yielded only two modes, as against the four to five modes for females. Final samples (B), however, resulted in three discrete modes for males. The convergence of the two lines representing the largest males agrees well with the concept of a maximum size reached by that sex. Means, standard deviations, and sample sizes are as shown in Figure 3.

### Sex ratio curves

An earlier analysis (Wenner, 1972) revealed that sex ratio may vary with size in marine Crustacea. At the time, such variation was believed to form a pattern characteristic of a species or population. It is clear from more recent results obtained from mole crabs both in Hawaii and Enewetak that the "characteristic pattern" hypothesis is now untenable. The data published in 1972 indicated an "intermediate" sex ratio pattern for *Hippa pacifica* in Hawaii, but data gathered later at Enewetak in 1972 yielded a "reversal" sex ratio pattern for the same species (see Fig. 5A).

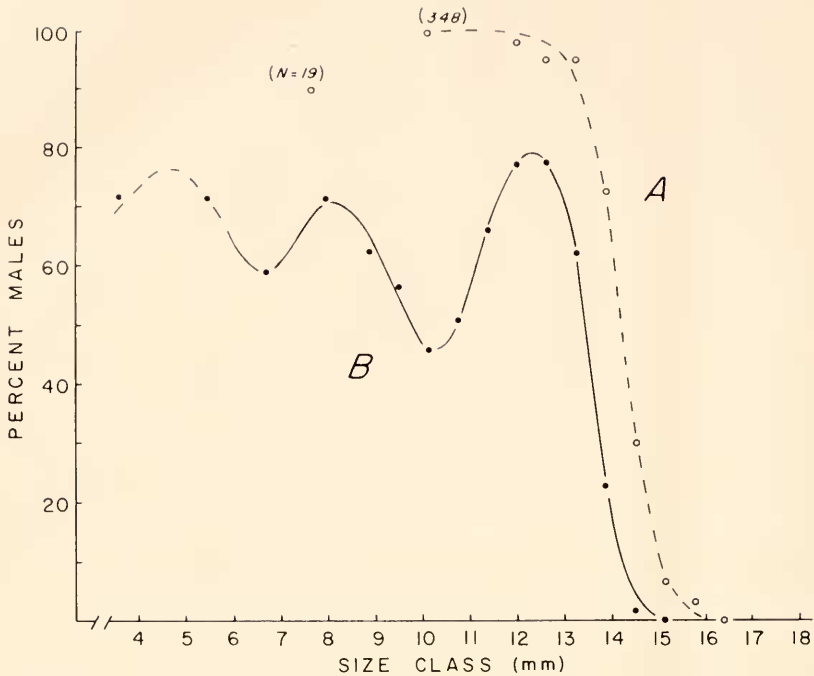


FIGURE 5. A discrepancy between sex ratio curves (sex ratio as a function of size—Wenner, 1972). A sigmoid curve (“reversal pattern”) was obtained in 1972 when approximately 2000 animals were collected from six beaches on five different islets (A). A new pattern (“oscillation pattern”) emerged when 4011 animals were removed from a single beach in the present study (B). Out of several hundred small animals in 1972, only one was female (the first point in Fig. 1A).

Data for initial samples in the current study yielded neither the Hawaii nor the earlier Enewetak sex ratio patterns; a sex ratio pattern existed which had not been found earlier (Fig. 5B). Instead, the percentage of males oscillated with increase in crab size. It is further evident that the number of oscillations corresponded well with the basic number of modal size classes found for males and females in the comparable size ranges (*i.e.*, Fig. 2).

The “oscillation” sex ratio pattern is what one might expect if the following conditions apply: first, the population consists of different cohorts which have arrived at different times from the plankton (three recent cohorts in this case), second, one sex grows faster than the other (females in this case—see Haley, 1979), and third, one sex reaches a maximum size, while the other sex continues growth beyond that size (females in this case).

For the first three samples of the present study, the sex ratio curve formed by the data for all animals greater than 10-mm carapace length nearly exactly matched that same portion of the curve for the total number of animals collected, as seen in Figure 5B. For the 86 animals in the first three samples which were 10 mm and smaller, however, only 28% were males, a point which falls far below

any of the points on the curve for all animals. This result corresponds with the under-representation of males as seen in Figure 4.

Despite the large discrepancy between sex ratio curves at the two localities and in different years, it should be noted that the sigmoid portions (for animals larger than 12 mm carapace length) of the curves in Figures 5A and 5B differ from one another by only about  $\frac{3}{4}$ -mm carapace length at the 50% level in the graph. The mean maximum size of males (12.5-mm carapace length) also falls close to that same level. It is also noteworthy that an analysis of *Hippa cubensis* data (from Hanson, 1969) places that portion of the curve for his species between the two curves shown in Figure 5.

#### *Size at onset of egg production*

The mean minimum size of egg production can be a useful measure in population studies if one wishes to compare the success of animals which live in one habitat with the success of animals which live elsewhere (Wenner, Fusaro, and Oaten, 1974). It is essential, however, that initial sample data accurately represent the entire population before one makes that comparison. (In decapods the mean minimum size at which females can extrude eggs is one convenient measure of sexual maturity, provided conditions are optimum for egg production, since eggs are usually retained on the pleopods until they hatch.)

Unfortunately, samples of *Hippa pacifica* populations in both Hawaii and at Enewetak taken in earlier years did not permit a determination of the mean minimum size at which egg-bearing occurred because small females were seldom caught. The previous sections document one possible reason for such a failure—samples taken early in the sampling period did not include an accurate representation of small females present in that population.

The removal of a larger percentage of the population in the present study produced a sizeable number of smaller females and permitted the derivation of a curve which represented the mean minimum size of egg production for this particular beach ( $\bar{x} = 12.4 \pm 1.02$  mm;  $N = ca. 1000$ ). The curve had a striking similarity to the shape of a comparable curve published earlier for *Emerita analoga* (Wenner, Fusaro, and Oaten, 1974).

A question remained as to whether initial samples would indicate a different size at onset of egg production than would data for the population as a whole. Consequently, data for the first three samples combined were compared to the data for the total 3-week catch. Although the available sample size for the early data was quite small (and although more scatter existed among the points), it was evident that a marked difference did not exist between early samples ( $\bar{x} = 12.7 \pm 4.64$  mm;  $N = ca. 150$ ) and total data in this comparison. Only 0.3-mm carapace length difference existed between means for best-fit lines from all data compared to data for only the first three samples.

#### DISCUSSION

Pacific mole crabs (*Hippa pacifica*) apparently live only in the intertidal zone (Wenner, 1977); the same habit was reported for *Hippa cubensis* by Hanson

(1969). (However, see Borradaile, 1906.) This restricted habitat, together with a behavior of readily coming to bait, makes these animals particularly suitable for studies of crustacean biology. Large numbers of these carnivores can be collected in a relatively short time. In addition, the animals can be measured quite rapidly while still alive by means of a graded sieve (Wenner, Fusaro, and Oaten, 1974). In the present study, these combined attributes permitted measurement and removal of a large percentage of Pacific mole crabs from a beach limited in length. From population estimates (Table I), based on changes which occurred during sampling (Southwood, 1966), it would appear that approximately 90% of the animals which inhabited that short stretch of beach on Enewetak Islet, Enewetak Atoll had been removed.

Some of the contrasting results between first and last samples were unexpected, in the sense that earlier (1970-71) samples had yielded repeatable data. At that time samples from different beaches or islets were very similar, and repeated samples (sampling with replacement) from the same beach matched one another. In retrospect, one might conclude that the sampling bias could have been anticipated, since animals were caught by "trapping" (*e.g.*, Gilbert, Gutierrez, Frazer, and Jones, 1976).

Trawling for animals can apparently lead to problems similar to those posed by trapping with bait. Gotshall (1972), while sampling shrimp during a 4-year period, experienced a bias problem similar to that encountered in the present study.

Small animals were caught less frequently at first and were primarily males; this discrepancy led to an imbalance in sex ratios throughout the sampling program. Hanson (1969; p. 15) earlier found such a discrepancy in his sampling program with *Hippa cubensis*. He wrote: "Length-frequency distributions of the (trapped animal) samples showed close conformation to those obtained by the more exact procedure of sieving sand samples from different levels of the beach, except for the smallest crabs (4-8-mm carapace length). Only 17.8% of the Bellair (trapped) samples were in this size range while 39.2% of the crabs from the Paynes Bay sieved samples were in this range." By contrast, Hanson derived an overall figure of 48.3% males for the animals from the several Paynes Bay beaches from initial samples, identical to the percentage we finally obtained only after removing more than 4000 animals from *one* beach. In addition, the first few samples in this present study were remarkably similar to one another, and by then 23% of the total catch had been removed. It was not until the fourth sample that a marked change in catch pattern occurred.

Although some changes during sampling were appreciable, the overall effort provided a rare opportunity: comparing all of the data from the removal beach with data obtained from the first few samples.

In studies of crustacean populations, a number of measures can assess just how discrete populations differ from one another in response to differences in environmental influences, but one must first have some confidence that initial samples have provided an accurate estimate of population characteristics before comparing populations with one another. Among the measures one can use are: first, modal size classes, including number of each sex in each size class and percentage of animals within each mode; second, size at onset of egg production (Wenner, Fusaro, and Oaten, 1974); third, extent of egg production, including

percentage of females carrying eggs and number of eggs per given size of female; fourth, "instantaneous" growth rate (Fusaro, 1978a), including field molt rate and size increment at molt; and fifth, sex ratio patterns (Wenner, 1972), including shape variations and pattern displacement. Age is generally not used, since that measure is very difficult or impossible to determine directly for crustaceans in nature (Wilder, 1953).

This current study has shown that initial samples provided reliable data for most of the above measures, but not all aspects, as discussed below.

Overall, the percentage of males and females within the different modes in the first three samples did not accurately represent the population structure obtained during the entire sampling program (Figs. 3, 4). Neither small males nor small females were properly represented in those first samples. Also, the seven large females caught at first were apparently the only very large animals on the beach.

However, although the percentage of males and females within each mode changed drastically during removal, the mean size of animals within each mode did not change appreciably (Figs. 3, 4). This means that population samples for this species can be compared to one another through time, if one takes into account the fact that the absolute percentages can vary greatly within each mode.

The first three samples yielded a reliable estimate for mean minimum size of egg production (Wenner, Fusaro, and Oaten, 1974), when compared to that estimate obtained in later samples or to that obtained from the total data (12.4-mm carapace length). Hanson (1969) found a 15-mm carapace length for the same characteristic in *Hippa cubensis*.

It is not yet certain whether the percentage of mature females which bears eggs is reliably determined from initial samples, but this seems to be the case. At the primary removal beach (Fig. 1D), an estimate derived from the first two samples (64.2%) was significantly lower than that obtained from all remaining samples (85.0%). However, data obtained from Jedrol Islet were quite consistent; the percentage of larger females (females greater than 12.4-mm carapace length) bearing eggs did not change during removal. It is therefore possible that an influx of food had occurred just prior to the beginning of sampling at the removal beach on Enewetak Islet (see Wenner, 1977, Table I). If so, it may be that the rising percentage of ovigerous females reflected that particular energy input.

At the removal beach, the sex ratio pattern (sex ratio as a function of size) obtained from initial samples quite clearly did not characterize the species or population as suggested earlier (Wenner, 1972, p. 344) for at least two reasons: first, small animals did not come to the bait in proportion to their numbers in the population when removal was begun; and second, it is now apparent from other work that both shape and position of the sex ratio curve can differ between populations and at different times of the year (see Fusaro, 1977).

A striking contrast between various Hawaii results (Wenner, 1972, Fig. 10; and Haley, 1979, Fig. 2) and Enewetak data (Figs. 5A, B, this study) can now be reconciled. The "intermediate" (Wenner, 1972, Fig. 10), "reversal" (Fig. 5A, this study), and "anomalous" (Haley, 1979, Fig. 2) sex ratio curves obtained from initial samples at various times likely did not accurately represent that aspect of population structure for the small animals. Rather, the differences between these patterns in the lower size classes probably reflect the degree to which



small animals had not been captured or the degree to which they might not have been seen during hand catching (Haley, 1979).

Three out of four of the previously described types of sex ratio patterns (Wenner, 1972) have thus now been obtained for a single species, apparently reflecting both sampling bias and changes in population structure. It is further apparent that each of those curves probably represented part of yet another sex ratio pattern (an "oscillation" pattern, Fig. 5B), a pattern which has now also been found for a confamilial mole crab, *Emerita analoga* (Fusaro, 1977). Furthermore, the number of oscillations in that pattern matches the number of major modal size classes found for males and small females (see Fig. 2), oscillations which may represent the number of major influxes of young in the recent months or years, modified by a differential growth rate between sexes (Haley, 1979).

In retrospect, it would appear that points which deviate from the sex ratio curve for other crustaceans (see Fig. 11 for *Calcinus latens* in an earlier analysis—Wenner, 1972) could well represent real deviations.

The results of this study indicate that males reach a maximum size in this species, a parameter which could be quite valuable for comparing populations one with another. In such comparisons, however, the largest male which can be found in each population is not the best estimate of that parameter (the "largest male size" normally increases with sample size). Rather, one can use the 50, 95, or 99% level in the mode representing the largest males. In Figure 2 the corresponding values would be:  $12.5 \pm 0.59$ , 13.8, and 14.3, respectively. Statistical comparisons between populations are feasible, of course, only if one uses the first of these estimates (because one then has an estimate of standard deviation).

The initial three samples provided an accurate estimate of mean maximum size of males when compared to the data for all males. The first three samples combined yielded a mean and standard deviation of  $12.4 \pm 0.48$  mm carapace length ( $N = 200$ ); the remaining large males had a comparable mean of  $12.5 \pm 0.52$  mm ( $N = 479$ ).

The fact that males reach a maximum size while females continue growing beyond that size provides a related measure for comparing populations: an arbitrary point on the sigmoid portion of the sex ratio curve, where females first become dominant in the larger size classes ( $13.7 \pm 0.47$  mm at the 50% level in Fig. 5B). Since these sigmoid portions of the sex ratio curve are straight lines on probability paper, one can derive an estimate of the mean and standard deviation for that 50% transition point. This transition size was also quite accurately determined from initial samples. The first three samples yielded values of  $14.0 \pm 0.73$  mm carapace length ( $N = 393$ ), compared to the overall value shown above of  $13.7 \pm 0.47$  mm ( $N = 745$ ).

Southwood (1966) outlined methods by which some systems might be sampled so as to reduce the amount of bias inherent in estimates of population structure. Gilbert, Gutierrez, Frazer, and Jones (1976, p. 57) updated the approaches outlined and admonished: "The sample must represent the defined 'population' of animals or plants we wish to investigate." The concern of these workers has been supported only in part by the current study. Initial samples did accurately represent some aspects of population structure. It should also be stressed that researchers who would like to understand crustacean biology better are not merely "choosing suit-

able species for ecological work" (Gilbert, Gutierrez, Frazer, and Jones, 1976, pp. 58, 59). Marine forms can often be readily caught *only* by some form of trapping (*i.e.*, bait, nets, etc.). Although there is perhaps no way to know if initial samples contain a bias without going through a removal process, it is also obvious that a bias can be tolerated once one knows its nature.

Other researchers have reported similar discrepancies. In an extreme example, Bolin (1961) found that plankton hauls caught only female lantern fish (*Tarleton-beamia crenularis*), while albacore tuna stomachs contained males but no females. The discrepancy became partially resolved when an unexplained event caused a massive death, resulting in millions of these fish being washed onto the beaches in central California. Of 521 specimens examined, 43.25% were males. Bolin speculated that males, being faster than females, could escape plankton nets. Conversely, he felt that females, having no photophores, would not be seen by tuna at that depth and could escape that mode of predation.

In a less extreme but still significant example, Gotshall (1972), who found marked discrepancies in catches of *Pandalus jordani* with respect to some year classes (size classes), suggested possibilities for those anomalous results, and reviewed some similar problems encountered by other researchers.

In the present study, although initial samples did not accurately portray a few of the conventional measures used by population biologists, reasonable estimates were gained of several parameters, as outlined above. The present study thus demonstrates the value of comparing data obtained from initial samples with actual population structure, especially when a biased sampling technique is the only feasible way to capture a sample from a population.

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#### SUMMARY

1. Essentially all of a population of mole crabs (*Hippa pacifica* Dana) was removed from an isolated beach at Enewetak Atoll, Marshall Islands. Estimates of population size, based on catch pattern, indicate that 87 to 93% of the animals were bait-trapped out of their restricted habitat. The sequential trapping permitted a number of comparisons between initial sample data and actual population structure.

2. The first three samples were large and yielded highly consistent data when compared to one another, but some aspects of population structure were nonetheless non-representative. For example, the percentage of crabs within each modal size class in the total population differed markedly from that estimated by initial samples. The location of those modal size classes did not change during the removal process.

3. After the first three samples (where male percentages were about 29%), sex ratio fluctuated wildly in individual samples, apparently as a consequence of size discrepancy in arrival at the bait. Eventually, males comprised about 48.4% of the 4011 animals removed.

4. Several other aspects of population structure were accurately estimated in early samples, including: mean size at onset of egg production, percentage of mature females carrying eggs, the sex ratio-size class relationship (for larger crabs), and the mean maximum size of males.

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